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The influence of social experience on the ontogenetic change in the relation between aggression, fear and display behaviour in black-headed gulls

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Abstract. This study investigated whether changes in motivation of displays, occurring during normal ontogeny in black-headed gulls, *Larus ridibundus*, are under the influence of social experience. To this end, birds were rearerd either in isolation or in groups of three. In the latter, the birds had social interactions, but did not show agonistic behaviour. The development of overt aggression and display behaviour was tested with a standard stimulus object, namely a stuffed or a live adult conspecific. In several aspects, the change in relation between aggression, fear and display was retarded in the experimental birds compared with that of control birds reared in a large group of at least nine birds. After re-housing in similar large groups, birds reared in isolation showed persistent deviations in frequency and orientation of agonistic and sexual behaviour. It is argued that the changes in motivation of display during ontogeny are influenced by specific experience with agonistic interactions, and may involve learning based on operant conditioning.

This study is part of a project undertaken to investigate the mechanisms underlying the development in form and context of species-specific stereotyped motor patterns used in social interactions. In this paper we deal with the influence of social experience on the change in context of certain displays in the black-headed gull, *Larus ridibundus*. In this species changes in the relation between aggression, fear and display behaviour occur during the course of normal ontogeny (Groothuis 1989b). In young black-headed gulls three species-specific displays are clearly part of agonistic behaviour: the oblique (an erect posture accompanied by a series of harsh and loud notes of decreasing duration), the forward (in which the neck is extended and the head is held in front of the body and the bill is held horizontally) and choking (in which the bird tilts towards the ground, while pointing the bill downwards and making a soft vocalization of short notes in rapid succession). These motor patterns gradually develop in form and frequency in the course of the first 10 weeks of age, in concordance with the development of overt aggression and fear behaviour. Furthermore, these young birds perform the displays exclusively in a clearly agonistic context, often during sudden switches between running towards and running away from the opponent, and in temporal sequences with overt aggression and fear behaviour. In addition, both aggression and the displays increase in frequency as the result of testosterone implantation, indicating that in young birds both aggression and display share an internal causal factor. However, in contrast to young birds, adults frequently perform the same displays without any overt aggressive behaviour, often during quiet approach towards the opponent and outside the agonistic context. Furthermore, adult gulls frequently show the displays at times when their production of testosterone is likely to be very low. In addition, and also in contrast to young birds, adults often time the oblique and forward displays very precisely simultaneously with the same display of the opponent, suggesting that for the causation of these displays specific external factors become more important than specific internal factors. These and other findings all indicated that the relation between aggression, fear and display changes in the course of ontogeny. It was concluded that the displays, once they have been developed and become fixed in form during ontogeny, become relatively independent of a specific internal state for agonistic behaviour.

Our aim in this study was to investigate the mechanisms responsible for these changes in the context of display behaviour. For two reasons

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experience with social interactions was expected to play an important role in these mechanisms. First, display behaviour in young black-headed gulls is performed exclusively in social interactions with conspecifics. Second, deprivation of social interactions can severely distort the development of agonistic behaviour (e.g. Kruijt 1964; for a review see Huntingford & Turner 1987). To investigate the influence of social experience on the development of agonistic behaviour two kinds of experiments were carried out. (1) To exclude entirely the influence of social experience with conspecifics, young gulls were reared in visual isolation from other birds. (2) To investigate whether abnormal agonistic behaviour in these isolated birds was due to lack of social experience in general, or to lack of agonistic interactions in particular, birds were reared in small groups. In such groups, birds clearly behave socially, but hardly ever perform agonistic behaviour (Groothuis 1989a).

The development of agonistic behaviour was tested with standard stimulus experiments in which a stuffed or live black-headed gull was introduced into the home cage, simulating an intruder on the territory. We concentrated on the following two types of behavioural phenomena which are indicative of the change in agonistic behaviour during ontogeny (Groothuis 1989b). (1) The shift in social behaviour from overt attack to display postures, clearly present in the ontogeny of birds reared in a large group, was studied in birds of the two experimental rearing conditions (isolated and in small groups). (2) The temporal relation between different locomotion categories and the timing of displays during these categories was also investigated. During normal ontogeny the frequency of alternation between overt attack and escape is initially high but then drops considerably. In older young gulls sudden switches between aggressive approach and escape become frequently interrupted by interjacent stops, during which the displays are performed. In adult birds such sudden stops occur much less frequently, and the display is often performed while the bird is standing still or is approaching the opponent quietly. These aspects were therefore studied in birds reared in isolation.

We also tried to test experimentally the conclusion (Groothuis 1989b) that the oblique, forward and choking postures in young gulls occur only in a clearly agonistic context.

EFFECT OF SOCIAL ISOLATION

Methods

Experimental groups and rearing conditions

The influence of social experience with conspecifics on the development of agonistic behaviour was totally excluded in 17 birds reared in visual isolation from other birds. From the age of 1–5 days after hatching, the birds were kept individually in indoor cages of $0{\cdot}5 \times 0{\cdot}5$ m until the age of 4 weeks, when they were isolated in outdoor cages, measuring 2×1 or 3×1 m.

Eight birds were used as controls (group-reared isolates). They were reared from hatching in large groups of at least nine individuals. In these groups many agonistic interactions occurred. Between the ages of 4 and 8 months, they were isolated in the same kind of outdoor cages as the experimental birds. In addition, data collected from mutual interactions of group-reared birds of several age classes, given in Groothuis (1989b), were used (group-reared controls). These latter birds are also referred to as 'normally reared birds'.

Eggs and 1–5-day-old chicks were collected in the field. All birds were fed mainly with mink or trout pellets, mixed with water for young birds. Chicks were stimulated to eat during their first 2 weeks of age by offering them some food on the top of a small stick. Water in the bathing pools, present in each cage, was replenished at least three times a week.

Tests

To study the effect of complete isolation on the outcome of the development of agonistic behaviour at an age when gulls reared normally in large groups have completed this development, agonistic behaviour was scored when the birds were 10 months old. The birds reared in isolation and the group-reared isolates were confronted with a live adult conspecific for about 15 min in their home cages. The wings of this stimulus bird were clipped, to prevent it from flying through the cage and avoiding the experimental bird. The stimulus bird behaved neutrally in that it showed neither aggression nor display behaviour. The behavioural interactions were video-recorded.

We used a living stimulus bird in these tests because chicks older than 4 weeks hardly ever respond aggressively to models. We did not separate the stimulus and experimental bird with a wire partition because such a separation seemed to prevent normal interactions between the birds and did not induce sufficient agonistic behaviour. The tests were kept as short as possible and were carried out in accordance with the Dutch law on animal experiments. In a few cases we stopped the tests because we felt the isolated bird was too aggressive towards the stimulus bird (more than 10 aggressive pecks in a single test or grasping the bird for more than a few seconds). After the tests, we did not notice harmful effects on the plumage or behaviour of the stimulus bird.

For a further study of abnormalities in social behaviour of isolated birds, and to investigate the stability of these deviations, all birds were placed in large groups of at least 10 birds with group-reared conspecifics, 1 or 2 months after the tests. These conspecifics had been reared in similar large groups and their age ranged from 1 to 4 years. Social interactions in these mixed groups were followed for more than 1 year thereafter for at least 50 h spread over 1 year.

We concentrated on the occurrence of the most frequently performed display in the black-headed gull, the oblique: an erect posture accompanied by a series of harsh, loud notes, the long-call. Aggression was scored when the birds pecked aggressively at the stimulus bird (for a more detailed description of the behaviour see Groothuis 1989a, b).

Results

Individual frequency of aggression and display

The individual frequencies in the 15-min tests of aggressive pecks and of oblique display of the birds reared in isolation were positively correlated ($r_S = 0{\cdot}63$, $N = 17$, $P < 0{\cdot}01$; Fig. 1). This suggests that in these 10-month-old birds oblique display and overt aggression still share a common causal factor.

Such a relation between aggression and display was hard to establish in isolated birds outside the tests, owing to the lack of a particular stimulus object to which they could direct aggression. However, approximately half of the birds occasionally performed display when alone in their home cage, and three of the most frequently displaying isolated birds frequently interrupted their display with aggressive pecks, directed to their own body. Two conclusions can be drawn from these findings. (1) The occurrence of both aggression and display in complete isolation, not evoked by a clear change in the external stimulus situation, indicates that the common causal factor for these two behaviour patterns lies within the animal itself. (2) Social isolation influences the orientation of aggressive behaviour.

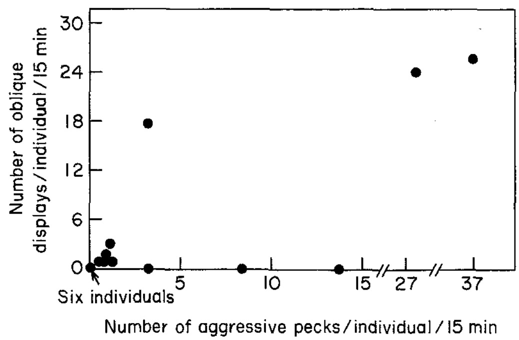

Figure 1. Correlation between the frequencies of aggressive pecks and oblique display of 10-month-old gulls, reared in isolation, and confronted with an adult conspecific in their home cage. Each point represents one individual except where stated otherwise.

Shift from overt aggression to display

The influence of social experience on the shift in social behaviour from overt aggression to display was analysed as follows. For each test the ratio of the frequency of aggressive pecks to the sum of the frequency of aggressive pecks and the frequency of oblique display was calculated. If social experience influences the decrease in the proportion of overt aggression in agonistic behaviour, this ratio should be relatively high in birds reared in isolation from early on compared with that of the eight control birds (the group-reared isolates) and of birds reared normally (group-reared controls) of approximately the same age.

Among the 17 birds kept in isolation from early on 11 individuals responded to the intruder with either aggression or display or with both. For these 11 birds, already 10 months old, the average ratio was 0·57 (the total number of aggressive pecks and of oblique display was 170). This ratio is even higher than the score for the group-reared controls, which were only 15 weeks of age and which were reared in large groups (0·26, the total number of aggressive pecks and of oblique display = 295). Four of the eight group-reared isolates of 10 months of age responded with either aggression or oblique display or both. Their average ratio was

0·05 (total number of aggressive peaks and of oblique display = 43). This score is very similar to that of adult birds reared in a large group (the group-reared controls: 0·06, $N = 120$). It is clearly lower than that of birds isolated from early on. The ratios of the experimental birds and of the group-reared isolates, despite the small number of responding birds in each group, were almost significantly different (Mann–Whitney U-test: $U = 7{\cdot}5$, $N = 15$, $P = 0{\cdot}055$), suggesting an effect of rearing condition on these ratios.

The relatively high proportion of aggression in the behaviour of the isolated birds is also indicated by the finding that some of these gulls reacted so aggressively to the intruder that the experiment had to be stopped in order to save the stimulus bird from injuries and too much stress. Furthermore, these aggressive birds sometimes held the stimulus bird tight with the bill for several seconds; this was never seen in the group-reared isolates, nor in the group-reared control birds.

In conclusion, the results suggest that social isolation retarded the shift from overt aggression to display behaviour.

Locomotion and display

From two of the highly aggressive and strongly responding birds, kept in isolation, enough data could be obtained to study the alternation of aggression and escape. The probability that approach or attack was immediately followed by withdrawal, instead of by standing still, turned out to be twice that expected on the basis of random transitions between these patterns ($\chi^2 = 27{\cdot}68$, $df = 1$, $P < 0{\cdot}001$). In contrast to adults reared normally, these birds often jumped away immediately after having performed overt aggression, and this alternation gave the behaviour of these almost adult isolated gulls the 'unbalanced' appearance typical of young birds. This indicates that the lack of social experience retarded the normal integration of aggressive and fear behaviour.

This interpretation is in line with the following findings. The majority of the six isolated birds that showed neither aggression nor display to the intruder showed excessive fear behaviour: they kept as far as possible from the introduced bird, and often flew against the walls of the cage, trying to escape. Such a clear division into either very aggressive or very fearful birds was not seen in the eight group-reared isolates. The four birds performing aggression and/or display in this group hardly ever showed pronounced aggression (see above), while the remaining four did not show excessive fear behaviour: one bird even took a bath during the experiment.

Table I. Observed and expected (in parentheses) frequencies of oblique display during different categories of locomotion of gulls confronted with a standard stimulus object

	Young gull 1–10 weeks old	Normally reared adult	Isolated adult
Approach	38 (28·0)	61 (43·0)	10 (8·9)
Stopping	137 (46·3)	25 (25·2)	36 (17·3)
Standing still	52 (89·7)	18 (28·6)	18 (21·8)
Withdrawal + sitting	41 (104)	9 (16·1)	0 (15·9)
Total	268	113	64

The timing of oblique display during locomotion was also studied in the two strongly responding aggressive isolates. The same methodology was applied as in Groothuis (1989b): if standing still immediately followed approach or withdrawal, it was scored as stopping. If a bird changed its posture during stopping, the second posture was scored as occurring during standing still. The two birds, which were already 10 months old, still performed the oblique posture relatively frequently during stopping ($\chi^2 = 36{\cdot}3$, $df = 1$, $P < 0{\cdot}001$) as did young birds ($\chi^2 = 243{\cdot}3$, $df = 1$, $P < 0{\cdot}001$) in contrast to adults reared normally in large groups ($\chi^2 = 0{\cdot}01$, $df = 1$, $P < 0{\cdot}95$; Table I; data for normally reared adults are from Groothuis 1989b). This stopping consisted of (often sudden) breaks in the movement towards the intruder (often followed by attack), or away from the opponent (escape), suggestive of an ambivalent agonistic motivation. Adults reared normally perform the display during quiet approach of the other bird, often their partners or their own young. Thus, in adult birds reared in isolation, oblique display still seems to be controlled by internal factors for agonistic behaviour, in contrast to the display of adult gulls reared normally.

Other abnormalities

After being re-housed in large groups, the isolated birds showed several types of deviations in their social behaviour, which were not observed in the behaviour of the eight group-reared isolates. The majority of gulls, reacting highly aggressively during the 15-min test in isolation, went on behaving very aggressively in the large group: some of these birds temporarily maintained territories half the size of the large cage, despite the presence of nests of conspecifics in their area. Three isolates frequently showed self-directed aggression: they spun round and tried to peck themselves (sometimes successfully) in the carpal joints as they did earlier while in isolation. In the large groups they often performed display behaviour on their own, instead of directing it to other birds. Furthermore, at least some of the isolated birds did not react adequately to the behaviour of conspecifics: for instance, when approaching the bathing pool when it was occupied by another bird, they did not react to threat display by the latter, and showed in their behaviour no anticipation of the attacks of the opponent when trying to drink.

These deviations lasted for more than a year after re-housing, but almost disappeared in the course of several years. Ten of the birds finally succeeded in becoming paired. In three of these males abnormalities in the orientation of copulation behaviour were found: for example they copulated on the ground beside their partners.

Thus, social isolation can lead to quite persistent, though not irreversible, abnormalities in frequency, application and orientation of aggressive and sexual behaviour.

EFFECT OF LIMITED SOCIAL EXPERIENCE

Methods

Experimental groups and rearing conditions

Twelve birds were reared in a social situation, but one without the context for agonistic interactions. Preliminary field observations had revealed that siblings, although they clearly had social interactions with each other, showed no aggressive behaviour towards their nestmates. Therefore, we collected eggs in the field and reared the chicks from hatching in four groups of three individuals (three is the normal clutch size in this species), in visual isolation from other groups. They were kept in indoor cages, measuring 1 × 1 m, until the age of 5 weeks; thereafter they were placed in outdoor cages, measuring 2 × 2 m. Food and water were supplied as described above for the isolation experiment. We recorded the development of display and overt aggressive behaviour for 5 h a week during the chicks' first 14 weeks. As expected, the frequency of this agonistic behaviour turned out to be extremely low. For example, the mean frequency per h per individual of aggressive pecks during the first 8 weeks after hatching was 0·04. This was much lower than the 0·74 for young gulls reared in a semi-natural condition (young gulls reared by their parents in a large aviary containing several breeding pairs).

Control group

Seventeen chicks were collected in the field when 3–5 days old, and reared together in an indoor cage of 3·5 × 1 m until the age of 4 weeks. Thereafter 12 of these birds were placed together in an outdoor aviary of 3·6 × 1·8 m. Black-headed gulls kept in these conditions form small subgroups of two to four individuals within a large group, each defending against other subgroups their own part of the cage and, during bathing, the water pool. This resembles the field situation, in which groups of siblings defend their territory against young gulls of other, neighbouring nests. Consequently, the control birds had many agonistic interactions with each other. Probably because of their high density, they had roughly twice as many interactions as birds reared in a semi-natural condition (see above).

Tests

We tested the development of agonistic behaviour of the experimental and control birds as follows. The birds in two of the four experimental groups and the large control group were tested weekly for about 15 min with a standard stimulus object, simulating a conspecific intruder on the territory. Two stimulus objects were used: a stuffed and a living adult black-headed gull. The stuffed bird was used during the first 7 weeks of age. It was mounted on the end of a long stick, and it was moved slowly through the whole cage. While the young gulls showed display or aggression in response to it the model was held more or less stationary. Because gulls older than 6 weeks were scared by dummies, from the time they were 5 weeks old a live adult conspecific was used as a stimulus object for agonistic behaviour. Between the age of 5 and 7 weeks, both stimulus objects were used, and the data combined. (For ethical and methodological considerations of such tests see the Methods section of the isolation experiment.) After the birds had reached the age of 11 weeks, they hardly ever showed agonistic behaviour in response to the test bird, and the series of tests was stopped. The test-bird, whose wings were clipped, behaved during the experiments rather 'neutrally' in that it showed neither aggressive behaviour nor display to the young gulls. All standard stimulus experiments were video-recorded. For every test the ratio of the frequency of aggressive pecks to the sum of the frequency of aggressive pecks and the frequency of oblique displays was calculated.

Additional information about the development of agonistic behaviour in the small experimental groups was obtained as follows. Each group of three birds was confronted with one of the other groups of three birds at the age of 15 weeks by removing the partition between two adjacent cages. The individual frequencies of oblique-like display and aggressive pecks were recorded during 8 h, spread over the first 3 days after removal of the partition.

Context of display

In a previous study (Groothuis 1989b) it was concluded that three of the four major displays of young black-headed gulls are motivated by agonistic tendencies, namely (1) the erect oblique-like postures; (2) the forward-like postures, in which the head is held in front of the body and the bill held horizontally; and (3) the choking-like postures, in which the bill is held down and the body often tilted towards the ground.

There was no relation between the begging or pumping display, in which the head is moved rapidly up and down, and aggressive behaviour. On the basis of this finding one would expect the three agonistic postures to occur only in an agonistic context, in contrast to the pumping display. We tested this expectation by comparing the frequencies of these displays and of aggressive pecks between two different situations: (1) interactions with the standard stimulus object, simulating an intruder on the territory; and (2) interactions between companions of the same small group.

Results

Context of display

As expected, the experimental birds showed almost no aggression towards other birds in the same group (Fig. 2). In this context, they showed mainly pumping movements and forward-like postures. In the 'intruder context', however, the frequency of aggressive behaviour increased considerably and significantly, as did the frequency of oblique-like, choking-like, and forward-like postures. The frequency of fear behaviour increased as well, but was not scored quantitatively. In contrast to the frequency of the other displays, the frequency of pumping did not change significantly. The apparent slight increase in this begging display is likely to be due to an increase in interactions between the group members, caused by a general increase in activity during the experiments. It can be concluded that oblique-like, forward-like and choking-like postures are most frequently performed in an agonistic context, in contrast to the begging display. This is in line with the above mentioned interpretation that in young birds in particular the first three displays are under the influence of internal factors, controlling overt aggressive and fear behaviour.

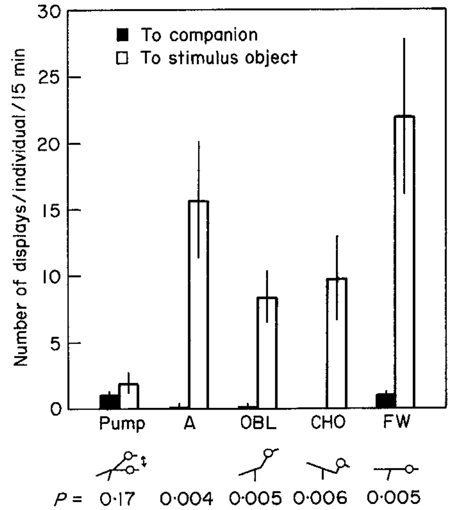

Figure 2. Frequencies ($\bar{X}\pm$SE) of four displays and aggressive pecking by young birds reared in small groups in two different contexts: towards companions in the same group and to a standard stimulus object simulating an intruder on the territory. *P*-values are derived from Wilcoxon matched-pairs tests. Pump: pumping (or begging); A: aggressive pecks; OBL: oblique-like postures; CHO: choking-like postures; FW: forward-like postures.

Shift from overt aggression to display

The slope of the regression line for the proportion of aggressive pecks of the large control

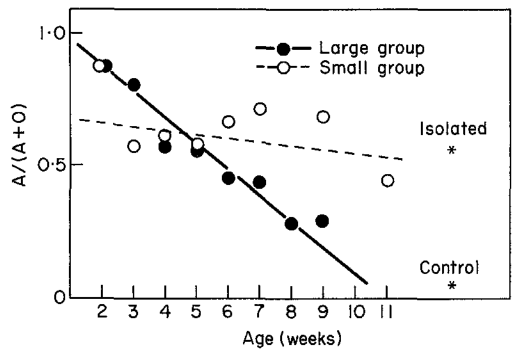

Figure 3. Ratio of aggressive pecks to oblique-like postures plus aggressive pecks (A/(A+O)) in weekly 15-min standard stimulus tests in one large and two small groups of young gulls. *: scores of 11 birds, isolated from hatching on, and of four control birds, isolated after several months of age, tested at the age of 10 months. See text for further details.

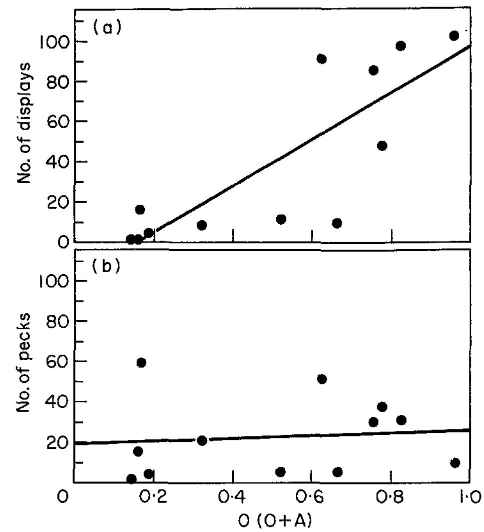

Figure 4. Correlation within individuals between the number of oblique display (a) or aggressive pecks (b), performed by birds reared in small groups recorded for 5 h per week during their first 14 weeks of age, and their ratio of oblique display to oblique display plus aggressive pecks (O/(O+A)) performed during 8 h in the confrontation test with unknown conspecifics in week 15.

group is significantly different from zero (T=9·73, df=6, P=0·015); this is not the case for that of the small experimental groups (T=1·38, df=6, P=0·22; Fig. 3). Because the birds in the small groups hardly ever had experience of agonistic interactions, in contrast to the gulls in the large group, this finding indicates that this kind of experience in particular is responsible for the decrease in overt aggressive behaviour during ontogeny.

The number of oblique-like postures a bird performed within its own group during its first 14 weeks of age was significantly correlated with the ratio of oblique displays to oblique displays plus aggressive pecks during the test at week 15, in which two groups were confronted with each other (Spearman rank-correlation: r_S=0·82, N=12, P<0·01; Fig. 4a). The number of aggressive pecks was not significantly correlated with this ratio (r_S=0·28, N=12, P=0·35; Fig. 4b). These results indicate that how much experience a bird has had with the effect of the performance of its own display influences the proportion of aggressive pecks in its agonistic behaviour during the test at week 15.

GENERAL DISCUSSION

The Influence of Social Experience: Possible Mechanisms

Our results confirm the conclusion from a previous study (Groothuis 1989b) that oblique-like, forward-like, and choking-like postures in young black-headed gulls can be considered as agonistic displays: they are performed exclusively in a clearly agonistic context (Fig. 2).

Both in birds reared in isolation and in birds reared in small groups, the development of agonistic behaviour was retarded. The experimental birds showed agonistic behaviour, in several respects similar to that of younger birds reared normally in large groups, and different from that of birds of their own age reared normally.

(1) The proportion of aggressive pecks in agonistic behaviour during the standard stimulus tests was higher in both types of experimental birds than in birds reared in large groups (Fig. 3).

(2) Overt aggression and fear still frequently alternated in some of the 10-month-old birds reared in isolation. Moreover, most of the birds reared in this condition were either highly aggressive or extremely fearful in response to an intruder in their home cage.

(3) In 10-month-old isolated birds, display still occurred very frequently in alternation with overt aggressive behaviour (Fig. 1).

(4) In some of these birds, oblique display was still performed during sudden stops after approach to or withdrawal from the opponent (Table I).

The first two findings have been reported for other animal species, reared in isolation. Kruijt (1964, 1971) reported excessive aggression, 'unbalanced' agonistic interactions and large individual differences in the social behaviour of isolated Burmese red junglefowl, *Gallus gallus spadiceus*. Some of these findings have been reported for the domestic cat, *Felis catus* (Baerends-van Roon & Baerends 1979), and for several fish species (e.g. Tooker & Miller 1980); for a review of abnormal aggressive behaviour in isolated animals of different species see Huntingford & Turner (1987, page 212). Apparently, aggressive behaviour can develop without social stimulation. The mechanism responsible for the development of overt aggressive behaviour in complete isolation needs further study.

Finding (1) indicates that social experience influences the shift from overt aggression to display behaviour, occurring in the course of normal ontogeny. From finding (2) it can be deduced that social isolation can retard the integration of motivational systems for aggressive and fear behaviour, underlying the final motor output. Kruijt (1964, 1971) also interpreted his findings in the behaviour of isolated fowl in this way. Findings (3) and (4) show that the increasing independence of oblique display from aggression and from ambivalently motivated stops did not occur in isolated birds. This might indicate that the increasing independence of display from an agonistic motivation, occurring in group-reared birds in late ontogeny, also depends on social experience.

The mechanism by which social experience determines properties of agonistic behaviour in the course of ontogeny is not yet clear. Excessive aggressive or fear behaviour of birds reared in isolation might be the result of these birds being tested with a stimulus object, until then unknown to them: a conspecific. The frequent alternation of aggressive approach with escape in some isolated birds could also result from this mechanism. These birds were highly aggressive and so relatively often found themselves close to the stimulus object, which then evoked fear.

However, the second finding indicates that habituation to conspecifics cannot be the whole story. Although lack of habituation may be the cause of excessive fear behaviour in isolated birds, it cannot explain the excessive aggression that occurred in birds reared in small groups of conspecifics. Moreover, because these socially reared birds lacked only experience with agonistic interactions, this type of interaction in particular seems to affect the development of normal agonistic behaviour.

There are, however, two other explanations that may account for the influence of experience with agonistic interactions.

First, it is conceivable that only in socially experienced birds does overt aggression gradually become inhibited by fear as a consequence of aggression by the opponent, provoked by attacks of the actor. Such a simultaneous activation of aggression and fear would result in a reduction in the frequency of overt aggression and an increase in the occurrence of display. In this case a bird learns to associate the opponent in an agonistic context (the conditional stimulus) with attacks by opponents (the unconditioned stimulus), resulting in arousal of fear in anticipation of these attacks (the conditional response). Such an arousal may then result in display behaviour if a tendency for attack behaviour was already activated.

Second, data obtained from the behaviour of birds reared in small groups indicate that operant conditioning should seriously be considered as an important contribution to the development of adult behaviour. Experience, in particular with display performed by the bird itself, was related to the shift from overt aggression to oblique display. This suggests that a bird might learn to replace overt aggression by display when it discovers that display is just as effective as overt aggression in inducing the opponent to retreat. By using display the bird might prevent a harmful escalation of interactions. The possibility that displays can be used as operants has been suggested earlier by Kruijt (1964) and Feekes (1972).

Classical and operant conditioning may act together in influencing the shift from attack to display behaviour. The increasing interaction between aggression and fear, leading to display, as a result of classical conditioning is likely to create the proper situation for operant conditioning of displays to occur.

As was mentioned before, findings (3) and (4) indicate that social experience may also influence the increasing independence of displays from motivational factors for agonistic behaviour, occurring in the course of normal ontogeny. In contrast to normally reared young gulls, normally reared adult birds perform display behaviour frequently outside a clearly agonistic context. Extension of the contexts in which the displays are employed, and consequently also extension of the original set of motivational factors underlying them, may also be due to operant conditioning. A bird may learn that the performance of its oblique display attracts females and its own young. The influence of operant conditioning on display performance, however, needs further experimental investigation.

Orientation of Social Behaviour and Persistence of Abnormalities

Self-directed aggression and/or abnormal orientation of sexual behaviour was found by Kruijt (1962, 1964, 1971) and Vidal (1982) in the behaviour of isolated fowl, and by Harlow & Harlow (1962) in the behaviour of isolated monkeys. Kruijt pointed out that isolated cocks directed their aggression towards their own tail which was the only moving object these birds could see. The importance of a moving object for the orientation of aggression is also indicated by the occurrence of self-oriented aggression in the gulls. It was directed at the carpal joints, the only moving objects the gulls could see.

It was remarkable that isolated birds developed aggressive behaviour at all, without the presence of social stimulus objects. Conceivably, experience with moving objects stimulates the development of aggressive behaviour. The persistence of self-directed aggression after re-housing in large groups, despite the presence of conspecifics, was unexpected, because such pecks may not be completely harmless to the bird and positive reinforcement for the maintenance of this behaviour is not obvious. The mechanism by which this abnormal orientation of aggressive behaviour became fixed needs further study.

The persistence of excessive aggression in some birds after re-housing might indicate that in older birds this behaviour becomes relatively insensitive to social experience. However, highly aggressive birds often won agonistic interactions, as a consequence of their excessive aggression. Therefore overt aggression may persist because it was often rewarded. Excessive aggression is also effective in winning interactions for young birds (Groothuis 1989b). One may wonder what function the shift to display behaviour has in group-reared birds, if excessively aggressive birds have an advantage for winning agonistic interactions. One reason might be that highly aggressive birds could not attract females or mate.

ACKNOWLEDGMENTS

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